CORRELATION OF PHYSIOLOGICAL DIVERGENCE WITH REPRODUCTIVE MODE IN CHAPARRAL SHRUBS

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ABSTRACT

Transpiration rates among chaparral species were found to correlate with mode of reproduction. Species of *Ceanothus* and *Arctostaphylos* that regenerate following fire only by seedlings were found to transpire on the average 2 times the rate of stump-sprouting species.

The correlation of these two life history traits suggested that other characteristics might also diverge among species of different reproductive mode. Data from the literature for water use, photosynthesis, and growth suggest that the divergence within *Ceanothus* and *Arctostaphylos* represents a fundamental change in species life-history; seedlings of obligate-seeding species may have been selected for rapid growth, exploitative resource use, and physiological tolerance of stresses during seedling establishment. Thus, obligate seeders may have seedlings with a better potential for establishment in comparison with seedlings of stump-sprouting species.

INTRODUCTION

Arctostaphylos and *Ceanothus* are among the dominants of the California chaparral and undergo regeneration of their populations following fire. In contrast to other chaparral genera, both *Arctostaphylos* and *Ceanothus* are characterized by two divergent reproductive modes. Species with the putative ancestral mode regenerate by resprouting from underground burls and by establishing seedlings (Wells 1969; Stebbins 1974, p. 180), whereas other species reproduce only by seedings. Some work has called attention to the ecological aspects of these genera and their reproductive modes in an effort to understand how the obligate-seeding species coexist with the putative ancestral form (Keeley 1977a,b; Keeley and Keeley 1977; Keeley and Zedler 1978). One central hypothesis of this work has been that the obligate seeder mode was a response to conditions favorable for seedling establishment (Keeley 1977a, Keeley and Zedler 1978). Other investigators have concentrated on differential flower production and pollinator attraction between these reproductive modes (Carpenter and Recher 1979, Fulton and Carpenter 1979).

The establishment of individuals during the juvenile stage is extremely critical and often determines the distribution of species within natural communities (Grubb 1977, Werner 1979). Germination and establishment of seedlings is rare and limited within established

chaparral (Christensen and Muller 1975b). Also, seeds of *Arctostaphylos* and *Ceanothus* species have dormancy mechanisms that usually restrict their germination to the first season or two following fire (Hanes 1977). This is the stage, along with density-dependent thinning within the next 10 years (Schlesinger and Gill 1978), that determines the degree of success for the obligate seeder. Selection might be expected to act differentially between these two reproductive modes at this life history stage, e.g., resulting in faster growth the first few years after fire among obligate seeders (Carpenter and Recher 1979). Because the juvenile stage is physiologically more sensitive to environmental conditions of the habitat (e.g., water stress; Schlesinger and Gill 1980), an adaptive physiological response would be critical for species with the obligate seeder mode.

This article describes divergence in a physiological characteristic, transpiration, that correlates with the established divergence in reproductive modes. Furthermore, I propose here that other aspects of growth and physiology may also diverge along with reproduction and suggest that the reproductive divergence within *Arctostaphylos* and *Ceanothus* represents an adaptive shift in the entire life-history among the derived, obligate-seeding species, rather than a change in reproductive characteristics only.

METHODS

The chaparral species in this study were collected from two sites in Marin County, California. Individuals used in the first three experiments were collected from a southeast-facing slope of a ridge off Pine Mountain. *Adenostoma fasciculatum* dominates on shallow, sandstone-derived substrates, along with *Arctostaphylos glandulosa, Ceanothus ramulosus, Heteromeles arbutifolia* and minor contributions from several other species. On adjacent shallow, serpentine-derived soil *Arctostaphylos montana* is found most abundantly along with *Ceanothus jepsonii, Adenostoma fasciculatum, Quercus durata* and minor contributions from several other species. On deeper soils, grasslands are found. Mixed sclerophyll forest species such as *Quercus agrifolia, Umbellularia californica, Arbutus menziesii* and *Pseudotsuga menziesii* sparingly occupy ravines along with chaparral on the southeast-facing slopes, but they dominate most of the northerly exposures. Mt. Tamalpais was the second site where chaparral species were collected from three adjacent, parallel, south-facing ridgetops. The first ridge was predominantly covered with *Arctostaphylos nummularia* var. *sensitiva* and *A. glandulosa* along with a shrub form of *Quercus wislizenii*. The second ridge was dominated by *Arctostaphylos canescens. Ceanothus foliosus, Arctostaphylos glandulosa* and *Adenostoma fasciculatum* were also found here. The third location was on a partially serpentine and sandstone-derived substrate and

contained *Arctostaphylos montana, A. glandulosa, Adenostoma fasciculatum* and *H. arbutifolia.*

Transpiration rates of 14 different species were compared using potometers. The first two experiments were performed during the drought season for these species. Field collections were taken on 17 September 1982 and 31 August 1983. The species were inactive in terms of growth or reproduction and were under considerable water stress. The second two experiments were conducted during the growing season, collections occurring on 1–2 February 1984. At this time the *Arctostaphylos* and *Ceanothus* species were initiating flowers or the buds were swelling. Only *Adenostoma* evidenced significant current-season vegetative growth. Field-collected branches were transported to the lab with their cut-ends submerged, immediately recut, and mounted underwater into erlenmeyer flasks with distilled water. The potometers were set up in a random-block design and left for two days under greenhouse conditions for the first two experiments and one day for the latter two. Conditions in the greenhouse varied considerably between experiments although the maximum air temperature remained between 30–35°C. Experiments I and IV experienced partly cloudly days including complete morning overcast that was prolonged during experiment I. Experiments II and III were conducted on days having a brief (II) or very brief (III) morning overcast followed by sunny conditions. Water loss was determined gravimetrically once daily and transpiration rates were calculated based upon leaf area. Leaf area was determined using the method of Mahall and Schlesinger (1982) modified by using photocopies of the leaves rather than using photographic proof paper. Five replicates were used in I, III, and IV and 6 in II. Statistical analysis was performed using a group-comparison "t"-test with log-transformed data (Zar 1974).

RESULTS

Because the environmental conditions of the greenhouse differed between experiments, absolute rates cannot be directly compared (Table 1), but a significant difference in transpiration rates does exist when stump-sprouting species are compared to obligate seeders. While some overlap does occur, obligate-seeding species transpired on the average at a rate twice that of stump-sprouters. This suggests that there has been a divergence among these species in their water relations that correlates with changes in reproductive mode.

The transpiration rates showed some additional patterns. The slowest rates were observed among species usually found in sclerophyll forests rather than chaparral (e.g., *Quercus chrysolepis, Umbellularia californica, Arbutus menziesii*) even though they may have occurred in "shrub-form" within chaparral stands. Among chaparral

dominants, the *Ceanothus* species consistently transpired at faster rates than the *Arctostaphylos* species despite the great variety of leaf size or shape and edaphic origin. All of the obligate-seeders transpired at several times the rate of most sprouting species with two exceptions, *Rhamnus californica* and *Adenostoma fasciculatum.*

Rhamnus was included in experiment II and transpired at a rate similar to that of *Arctostaphylos montana,* an obligate seeder. *Rhamnus californica* however, is locally more abundant in more mesic sites and seems to increase in abundance in fog-dominated sites along the coast (pers. observ.), and thus may be considered to be a plant of more mesic circumstances than typical chaparral. The transpiration rates of *Adenostoma fasciculatum* were always within the range of the obligate seeders. For *Adenostoma,* this was undoubtably a reflection of greater transpiration rates compared with other sprouters, but may also represent an overestimate to some extent due to two circumstances. One may be the method chosen to determine leaf surface area. More error can be expected when determining leaf area for small, terete needles than for larger, flat leaves. The results for each experiment were statistically significant ($p < 0.05$) even though these two species overlap in transpiration rates with obligate seeders (except for experiment IV). This could be due to the occurrence of substantial new growth on *Adenostoma* shoots while all the other species still had only previous season's leaves. In the last two experiments with *Adenostoma* branches containing new growth, the magnitude of the difference between *Adenostoma* and the other sprouters is much greater compared to the earlier experiments. Without *Adenostoma* included in the data analysis, the difference between rates of obligate seeders and sprouters is highly significant ($p < 0.005$ without *Adenostoma* for IV). *Adenostoma* will be discussed in more detail later.

Discussion

The obligate seeder mode of reproduction has been suggested to be an adaptive response to fire (Jepson 1939, Wells 1969), an environmental factor that has overwhelmingly shaped many of the characteristics of chaparral vegetation (Hanes 1977). Keeley and Zedler (1978) listed three life history characteristics important with respect to fire: 1) relative ability to survive fires; 2) relative ability to establish seedlings after fire; and 3) relative longevity and competitive ability between fires. Stump-sprouting species have a higher post-fire survival rate than obligate seeders. Although survival varies by species and location, at least some percentage of the stump-sprouting population survives fire (Horton and Kraebel 1955; Hanes 1971, 1977; Keeley and Keeley 1977, 1981) compared with complete elimination of obligate seeders. Comparisons of longevity have

yielded various results. Some work suggests shorter lifetimes for most obligate-seeding species (Horton and Kraebel 1955; Hanes 1971, 1977; Grant 1977, p. 272), although great relative longevity has been found for other species (Keeley 1975, Keeley and Zedler 1978).

Because obligate seeders seem to be at a disadvantage in regard to survival of individuals after fire, and, at best, neutral considering longevity, the inability to resprout in obligate seeders suggests there must be significant differences between these modes in seedling establishment. Keeley (1977a) and Keeley and Zedler (1978) proposed that the obligate seeder mode is a response to conditions advantageous to seedling establishment and showed that abundance and diversity of obligate-seeding species are positively correlated with longer intervals between fires. They suggested that these longer between-fire intervals allowed for thinning of shrubs in older stands, opening up larger gaps following fires for seedling establishment between resprouting shrubs.

There should be a differential advantage during establishment, however, among individual seedlings of obligate seeders over those of sprouting-species in order to maintain the obligate-seeding populations. It becomes necessary, therefore, to consider what characteristics would be required to convey a differential advantage at establishment. If there are no significant differences between seedlings of stump-sprouting species and obligate seeders, then seeders would be at an advantage only if they numerically dominated potential establishment sites. On the other hand, if seedlings of obligate seeders were physiologically superior with respect to establishment, then numerical dominance of buried seed reserves would not be essential. In general, greater reproductive allocation has been found among obligate seeders for numbers of flowers and nectar production (Fulton and Carpenter 1979) and seed production (Keeley 1977b). Following fires seedlings of obligate seeders have tended to be more abundant than those of stump sprouters (Horton and Kraebel 1955, Hanes 1971, Vogl and Schorr 1972, Keeley and Zedler 1978); however, these studies have investigated only a limited number of species. Keeley and Keeley (1977) found that reproductive effort in obligate seeders was not maximized early in the life history but increased with time, as in stump sprouters. In younger but mature stands (23 yr) there was no significant difference in vegetative or reproductive allocation between *Arctostaphylos glauca* (seeder) and *A. glandulosa* (sprouter). Furthermore, other comparisons between congeneric pairs in both *Arctostaphylos* and *Ceanothus* have yielded no consistent pattern between stump sprouters and obligate seeders regarding seed and fruit production, numbers of viable seeds in the soil, numbers of seedlings following fire, and post-fire seedling mortality (Keeley 1977b). Seed production may differ greatly between ecotypes and

be extremely poor in obligate seeders (Vasek and Clovis 1976). Seed production has also been variable and dependent upon weather patterns in all species examined (Keeley and Keeley 1977, 1981; Baker et al. 1982). The overall impression is that some obligate-seeding species may achieve seedling dominance by numerical superiority (e.g., *Ceanothus greggii*) but that this is not a consistent characteristic of species with this reproductive mode.

Alternatively, physiological superiority may provide the potential for successful seedling establishment. Post-fire conditions for establishment are initially favorable, particularly with regard to nutrient levels (Christensen and Muller 1975a), but quickly deteriorate due to growth of fire-response herbaceous and woody species (Horton 1950, Schultz et al. 1955) as well as to temperature and drought stress as summer approaches (Ammirati 1967, Hanes 1977). Physiological characteristics influencing growth under these conditions, particularly water use and carbon gain, should differ between reproductive modes if obligate seeders have an advantage at the level of individual seedlings. Most recent summaries of physiological work on chaparral species (e.g., Hanes 1977, Poole et al. 1981, Oechel et al. 1981) have not attempted to correlate physiological processes with reproductive mode, however, but instead have concentrated on characteristics of individual species or on comparisons among vegetation of different Mediterranean-type climates. The transpiration data from this study (Table 1) suggest a divergence among these species in their water relations correlated with changes in reproductive mode. Such a remarkable coincidence leads one to consider the likelihood of an integral relationship between the two processes.

Early suggestions concerning water use by evergreen species were that water use would be moderate, soil moisture would be conserved, and species would just be entering dormancy near the end of the drought period (Specht 1972a,b). As pointed out by Poole et al. (1981), this pattern is consistent with certain species only, e.g., *Adenostoma fasciculatum, Quercus dumosa,* and *Rhus ovata* (all stump sprouters), but not with *Arctostaphylos glauca* or *Ceanothus greggii*. These two obligate seeders differ in several ways from the stump sprouters. Poole et al. (1981) suggest that "in a competitive situation, a species captures and uses more water by using water lavishly when it is available, rather than by conservatively using water. Such a pattern exists in *A. glauca* and *C. greggii*." Also, they found both *Ceanothus greggii* and *Arctostaphylos glauca* maintained leaf conductances down to -6.0 MPa while sprouting species showed no conductance at higher levels of xylem tension (-2.0 MPa for *Rhus ovata* down to -5.0 MPa for *Adenostoma fasciculatum*). As chaparral species experienced increasing water stress during the summer drought period, Baker et al. (1982) reported *Adenostoma fascicu-*

TABLE 1. Transpiration Rates of Selected Species in g $H_2O/dm^2/Day \pm 1$ SE. Data analyzed by group-comparison "t"-test on log-transformed data: Exp I: $p < 0.05$, $t = 2.50$, df = 7; Exp II: $p < 0.05$, $t = 2.68$, df = 7; Exp III: $p < 0.05$, $t = 2.63$, df = 5; Exp IV: $p < 0.10$, $t = 2.18$, df = 6, without *Adenostoma*: $p < 0.005$, $t = 5.24$, df = 5.

	Experiments			
	I	II	III	IV
Stump-sprouters				
Adenostoma fasciculatum	10.47 ± 2.11	—	26.55 ± 2.36	19.84 ± 2.46
Arctostaphylos glandulosa	4.43 ± 0.73	13.90 ± 1.88	12.34 ± 2.27	7.76 ± 1.60
Heteromeles arbutifolia	6.54 ± 0.84	9.10 ± 0.82	9.95 ± 1.22	4.84 ± 0.51
Quercus durata	4.60 ± 0.48	6.00 ± 0.78	4.14 ± 1.03	—
Arbutus menziesii	4.92 ± 0.76	—	—	—
Umbellularia californica	3.73 ± 0.50	—	—	—
Rhamnus californica	—	18.70 ± 2.59	—	—
Quercus chrysolepis	—	—	—	3.38 ± 0.41
x̄ ± 1 SE	5.78 ± 1.01	11.92 ± 2.78	13.24 ± 4.76	8.95 ± 3.75
Obligate seeders				
Arctostaphylos montana	7.68 ± 0.92	18.20 ± 2.12	23.46 ± 0.65	15.30 ± 0.92
A. nummularia var. *sensitiva*	—	—	—	14.10 ± 0.93
A. canescens	—	—	—	17.52 ± 1.04
Ceanothus jepsonii	17.01 ± 1.19	30.30 ± 3.59	48.11 ± 4.36	—
C. ramulosus	9.38 ± 1.26	41.00 ± 4.36	88.34 ± 2.04	—
C. foliosus	—	—	—	20.28 ± 2.60
x̄ ± 1 SE	11.36 ± 2.87	29.83 ± 6.58	53.30 ± 18.91	16.80 ± 1.36

latum (sprouter) and *Arctostaphylos viscida* (seeder) ceased branch elongation when midday plant water potentials fell between -2.3 to -2.7 MPa, while elongation continued in an obligate seeder, *Ceanothus cuneatus,* down to -3.5 MPa. All these characteristics suggest that obligate seeders rapidly capture limited resources and have been selected to be competitive (sensu Muller 1969; or Grime 1979, p. 8). Furthermore, they can maintain physiological activity at the low water potentials certainly experienced by establishing seedlings (Schlesinger and Gill 1980). Because the obligate-seeding species have, in general, shallower rooting systems (Hellmers et al. 1955, Kummerow et al. 1977), these characteristics might be relatively advantageous largely at the seedling stage in a comparison with stump-sprouting species.

Higher transpiration rates tend to correlate with higher photosynthetic rates. A survey of published values for photosynthetic rates (Table 2) demonstrates a predicted divergence correlating with reproductive mode, obligate seeders having rates 2–3 times greater than sprouters. This divergence is remarkable because Table 2 combines field and laboratory findings that differ in season measured and in climatic features (northern vs. southern California; xeric vs. relatively mesic). In computer simulations, Miller (1981) also found that canopy photosynthesis was greater for the obligate seeders investigated (*C. greggii* and *A. glauca*) than the stump sprouters (*A. fasciculatum* and *R. ovata*) whether considered over ground area or leaf area. These photosynthetic rates suggest faster potential growth rates in obligate seeders, a contention supported by comparing seedling height data collected over a several year period for species of both reproductive modes (Horton and Kraebel 1955).

These data taken together suggest that the divergence within *Arctostaphylos* and *Ceanothus* does not, therefore, appear to be a change in a single or several reproductive life history characters, but instead, a set of traits forming an "adaptive combination" (Oka 1983). The reproductive divergence may well represent a fundamental change in species life-history within these two genera. Horton and Kraebel's (1955) data demonstrated the more rapid growth of obligate seeders at the seedling stage and support the hypothesis that the obligate seeder mode has been selected for a suite of characteristics in addition to large numbers of seedlings, such as rapid seedling growth, exploitative resource use, and physiological tolerance of stresses typical of seedling establishment (e.g., water stress). Thus, obligate seeders should have seedlings with a better potential for establishment in comparison with seedlings of stump-sprouting species. I have focused on physiological divergence at the seedling stage because establishment is essential for obligate seeders to persist in the vegetation. Faster growth and exploitative resource use would be advantageous for establishing chaparral seedlings. Such an advantage

TABLE 2. MAXIMUM RATES OF PHOTOSYNTHESIS (nmol $CO_2/cm^2/sec$) AS REPORTED FROM PUBLICATIONS. Values listed are maximum rates unless ranges were reported, in which case upper and lower values are listed. Letters following values refer to the source publication: a—Oechel et al. 1981; b—Oechel and Lawrence 1979; c—Mahall and Schlesinger 1982; d—Mooney et al. 1975; e—Harrison et al. 1971. [1]Data was analyzed by group-comparison "t"-test using log-transformed data: $p \ll 0.001$, $t = 5.58$, df = 22.

	Stump-sprouter	Obligate seeder
Adenostoma fasciculatum	0.221a	
	0.417a	
	0.461a	
Ceanothus leucodermis	0.455a	
Cercocarpus betuloides	0.429a	
	0.247e	
Quercus dumosa	0.391a	
Rhus integrifolia	0.271a	
Rhus ovata	0.284a	
	0.139e	
Rhus laurina	0.325e	
Heteromeles arbutifolia	0.253d	
	0.235e	
Prunus ilicifolia	0.289e	
Arctostaphylos glauca		0.480a
		0.663a
		0.802a
Ceanothus greggii		0.480a
		0.657a
		0.543a
		0.850b
Ceanothus verrucosus		0.524a
Ceanothus megacarpus		1.300c
		1.900c
x̄	0.315[1]	0.819[1]

may not be carried into the adult stage, however, as indicated by water use and carbon gain data over 12 month periods in mature stands (Poole et al. 1981, Oechel et al. 1981). In any case, while existing data seem to support the preceding ideas and a correlation between physiological and reproductive processes hardly seems coincidental, more data need to be collected, and on additional species, before more definitive statements can be made. Further complications may arise among species groups that have occupied xeric to more mesic habitats, or vice versa, through evolutionary time (Stebbins 1974, p. 179–181) or simply due to climatic differences in habitats.

Although obligate seeders and stump sprouters seem to constitute two distinct groups in terms of resource use and growth rates, they may also be regarded as different ends of a continuum, similar to the reproductive continuum suggested by Keeley and Zedler (1978). The middle of the continuum would consist of slower growing seed-

ers and faster growing sprouters. In this regard, special mention should be made of *Adenostoma fasciculatum*. This species had transpiration rates within the range of the obligate seeders (Table 1), leaf conductance patterns more similar to the seeders measured than to the other sprouters in one study (Poole et al. 1981), and photosynthetic rates at the high end of the sprouters (Table 2). *Adenostoma* not only resprouts effectively following fires but also establishes large numbers of seedlings (Horton and Kraebel 1955, Vogl and Schorr 1972, Keeley and Zedler 1978). Apparently, *Adenostoma* combines characteristics of both of these syndromes (sprouter vs. seeder) along with a dimorphic seed population composed of readily germinable and dormant seeds (Stone and Juhren 1953). *Adenostoma* is clearly the dominant species of lower elevation chaparral in California (Hanes 1977) and Cooper (1922) even suggested it was the "climax" dominant of the central coast ranges. This combination of characteristics in *Adenostoma* described above may account for the flexibility required to achieve and maintain this dominance.

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